Two New Species of *Hoffmannia* (Rubiaceae) from Panama, with Remarks on Circumscription of Mesoamerican Species of the Genus

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ABSTRACT. The unusual degree of variation within *Hoffmannia* populations and the difficulty in clearly defining some Mesoamerican species are discussed. Two new species, *Hoffmannia dwyeri* and *H. fortunensis*, both endemic to the Chiriquí highlands, are described.

Having worked with Hoffmannia for the Flora Costaricensis series (Burger & Taylor, 1993), it seemed appropriate to expand that effort and treat the genus for the Flora Mesoamericana project. Work with the Costa Rican material had indicated that most species in the genus were very variable morphologically, and that making specific distinctions in some groups was extremely difficult or arbitrary. Unfortunately, studying over 3000 specimens of Hoffmannia in the region covered by the Flora Mesoamericana has made these difficulties abundantly clear.

While individuals of most plant species vary considerably, there are usually concordant suites of consistent morphological traits that allow us to identify and distinguish species from their close congeners. Floral dimensions and morphology are usually sufficiently constrained so that they are useful in characterizing species. Leaf dimensions may vary greatly, but leaf form and venation patterns are usually also helpful in identifying and distinguishing closely related species. Many species of Hoffmannia, however, exhibit a wider-than-normal range of variation in both floral dimensions, vesture, plant size, and leaf size and shape. This wider range of variation is rarely exhibited by any one plant; it becomes apparent only when a larger suite of collections is gathered together.

We use larger suites of collections to assess population variation, characterize species, determine species differences, delineate ranges, and look for local or regional differentiation. If we are able to effectively separate congeneric material into two closely related species, and then find that they consistently grow in different areas or slightly different habitats, we are reassured that they are indeed different species. If we find a few collections that are

intermediate in a number of characteristics that distinguish two closely related species, both represented by large suites of collections, we may be confident that we have identified hybrids. If there are many intermediates between two distinctive morphological populations, we may be dealing with a cline or subspecific differentiation. In both these instances, however, we must first describe and characterize two different suites of character states, delimiting our species or subspecies. The problem in Hoffmannia is that the variation is often so great, and there is so little correlation between different characters, that delimiting two closely related "species" among a large suite of similar collections can be quite arbitrary. The only effective way to tackle this kind of problem is to separate out the most distinctive entities first, then try to tease out other distinctive taxa, before finally dealing with a large complex of similar specimens.

Clearly, one of the most easily distinguished species in the genus is Hoffmannia vesiculifera Standley, which has two inflated elongate vesicles along the lateral sides of the usually short petiole. Hoffmannia kirkbridei Dwyer also has such vesicles, but that species has very different petioles and leaf form, is known from only two collections, and may prove to be a variant of H. vesiculifera. Setting aside the two collections tentatively assigned to H. kirkbridei, and using the vesicles as a defining autapomorphy for H. vesiculifera, we can bring together a number of specimens that display a wide range of variation in both leaf and inflorescence characteristics. The plants themselves grow from 0.1 to 1.5 m in height when flowering, and range from central Costa Rica to central Panama. The inflorescences vary from sessile congested fascicles to pedunculate and distally branched paniculate forms. Leaves range from 10 to 30 cm in length and vary from elliptic to oblong or obovate. Calyx lobes may be 4-20 mm long; the corolla varies from about 10 to 20 mm in length. These extremes are never found on the same individual, and they do not characterize particular habitats, localities, or differing elevations. Rather, the extreme individuals appear

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to be nothing more than unusual variants. Some of the more distinctive variants have been the basis for erecting new species, but all can be linked with the earliest type through intermediate collections. In the eastern part of this species' range, inflorescences are often borne on peduncles with small leaves at their apex (modified axillary branches). In the same area, there are plants with flowers densely crowded in the leaf axils, as in the type of H. morii Dwyer, based on Mori & Kallunki 5915 (MO). At first, the two forms appear to be different species, but a larger series of specimens will include some with intermediate inflorescence characteristics. In short, H. vesiculifera appears to be a species easily identifiable by the petiolar vesicles, larger calyx lobes, generally short habit, and pubescence; but it is a species that varies rather dramatically in virtually all of its morphological features.

If we think of H. vesiculifera as being typical of Hoffmannia species, wide patterns of variation in other species of the genus become easier to understand. What gives us problems is the fact that these other species usually do not possess a similarly unique identifying trait. Hoffmannia vesiculifera and the poorly known H. kirkbridei Dwyer are the only species of the genus to have developed petiolar pouches large enough to house small ants. A number of species, such as the two new species being described below, do have a suite of distinctive traits and limited geographic range that make them relatively easy to recognize, but by the time we separate out such species we are left with wide-ranging taxa that may be catchalls for large numbers of similar-looking material.

Hoffmannia regalis (J. D. Hooker) Hemsley was based on horticultural material grown in Europe, and the name has been used for some wild collections from southern Mexico. The geographic origin of the original cultivated material was not known, but similar material of Hoffmannia is found only in Chiapas and Guatemala. The large leaves are occasionally broad and brilliantly colored with shades of purple beneath and a rich dark green above, the obvious reason for its introduction as a horticultural novelty. As in the case of H. vesiculifera, there is great variation in leaf size, shape, and coloring. Leaf bases, petioles, and inflorescences are also highly variable. The result of this extensive withinpopulation variation is that there is no way to clearly separate those specimens that have in the past been identified as Hoffmannia lineolata J. Donn. Smith and H. riparia Standley. This latter material has been distinguished by its more often elliptic leaves with well-defined petioles and a lamina base that is not so long-decurrent. A large suite of collections makes it clear that these differences are bridged by many intermediates at all elevations. While the large, broad, brilliantly colored leaves are only found at elevations above 1200 m, there is sufficient variation at all elevations to make recognition of more than one species dubious.

Hoffmannia subauriculata Standley is quite distinctive because of its long-tapering lamina base and winged petioles, but it also exhibits considerable variation. The winged petioles are usually rounded and subauriculate at the stem, but not always. The plants are often short in stature with inflorescences usually borne at the lower leafless nodes, even at rooting nodes. The species ranges from Costa Rica to Colombia. Specimens from Darién, Panama, are distinctive because their consistently oblanceolate leaves tend to dry grayish, and their winged petioles are not auriculate at the base. Also the stems are often horizontal and rooting along the proximal nodes in eastern Panama. The name H. eliasii Dwyer would be appropriate if these plants of eastern Panama were to be separated from H. subauriculata as a distinct species, but it seems best to consider them part of a single variable species.

An extremely variable complex is found in the Chiriquí highlands of Panama, for which the name H. pittieri Standley has often been used. These populations may intergrade with material referable to the earlier named H. arborescens J. Donn. Smith of Costa Rica's Talamanca mountains. I have separated these collections by annotating those with usually axillary branched or cymose inflorescences as H. arborescens, and those in which the flowering inflorescences are simpler and largely confined to the lower leafless nodes as H. pittieri, consistent with the types. Unfortunately, there are intermediate collections both as regards their inflorescences and in other characteristics. It may be that this complex of forms should be further divided according to specific morphological traits, but I suspect that this is unrealistic. A closer examination of the populations in Chiriquí, and especially their cytology, might help unravel this problem. There is a report of within-species polyploidy in Hoffmannia (C. M. Taylor, pers. comm.), and this may be a factor in the variability found within the genus.

The most commonly collected species of *Hoff-mannia* in Mexico and Central America is *H. ni-cotianifolia* (M. Martens & Galeoti) L. O. Williams. Based on material collected in Veracruz, Mexico, the name suggests plants with larger leaves. Among Veracruz collections there are large-leaved collections, a greater number of smaller-leaved collections, and some intermediates. Based on this vari-

ation in the region in which the earliest type was collected, I believe it is best to interpret *H. nicotianifolia* very broadly. However, adopting a broader interpretation can cause difficulty in dealing with distinctive variants that may be common in some geographical regions such as Honduras or Nicaragua.

A large percentage of Hoffmannia specimens from Nicaragua dry with a characteristic orangebrown or olive-green coloration and many have larger obovate to oblanceolate leaves. Their small flowers and short pedunculate inflorescences with thin pedicels clearly ally them with H. nicotianifolia. Because they are quite distinctive and characteristic of so much material from Nicaragua, they could be recognized as a separate species, first described by L. O. Williams as H. oreophila. However, with much variation and many intermediate collections, it seems best to include H. oreophila in a broad circumscription of H. nicotianifolia. This is consistent with also treating H. angustifolia Standley of Guatemala and Honduras as a synonym of H. nicotianifolia. After a review of many collections, I believe a broader, more inclusive species concept is justified, making H. nicotianifolia a species that ranges from northeastern Mexico to eastern Panama. However, larger circumscription does not eliminate the problem of having collections that appear to be intermediate with other closely related species. In the case of H. nicotianifolia there are collections that appear to be intermediate with H. cryptoneura Standley, H. excelsa (Kunth) K. Schumann, H. hondurensis Standley, H. laxa Standley, H. oreophila, H. pittieri, H. psychotriifolia (Bentham) Grisebach, H. regalis, and H. stevermarkii Standley. Whether any of the "intermediate" collections are true hybrid-like products of interspecific gene flow or simply variants with characteristics of one of the other species is difficult to determine.

Hoffmannia psychotriifolia is quite similar to H. nicotianifolia but differs from the latter by the usually longer corolla and by the consistently sessile inflorescences. The two are sometimes collected together. The names Hoffmannia rotundata Standley (holotype: Purpus 7268, MO) and H. chiapensis Standley (holotype: Purpus 7268, US) were based on a collection that Standley recognized as mixed. All the herbarium sheets seen have some elements of the two similar species. Having reviewed the descriptions and examined sheets from F, US, and MO, it appears that H. rotundata is a synonym of H. nicotianifolia in a wide sense, while H. chiapensis is a synonym of H. psychotriifolia. The type

sheets and their respective parts have been annotated accordingly.

In central Panama there are specimens of Hoffmannia nicotianifolia with more ovate leaves that have been identified as H. cercidifolia Dwyer by Dwyer. However, the type of H. cercidifolia (Duke 15597 (2), MO) was collected in Darién and appears to represent a different species. Unfortunately, the type has only a few subsessile immature flowers and provides insufficient information to come to any firm conclusion regarding its placement. In addition, there are no similar collections from Darién to give us a better idea of the population that this collection represents. It seems likely that the type of H. cercidifolia may prove to be an unusual collection of an earlier named South American species, but it will require better sampling of the Darién populations before that likelihood can be verified.

At present a draft treatment of *Hoffmannia* for the *Flora Mesoamericana* includes 49 species. Having accepted many broader species concepts, I have also tended to tentatively place unusual collections within a related described species rather than erect new names. However, two small groups of collections from the Chiriquí highlands appear to represent two new and distinctive species.

Hoffmannia dwyeri W. Burger, sp. nov. TYPE: Panama. Chiriquí: vicinity of Boquete, Cerro Pate de Macho, SW slope, 8°46′N, 82°25′W, 1800–1950 m, 19 June 1987, Croat 66403 (holotype, MO; isotype, F). Figure 1.

Species habitu cum *Hoffmannia valerii* Standley optime congruens, sed differt corollis longioribus, foliis basi cuneatis, petiolis alatis, stigmatibus latis, habitatione altitudo alta (1700–2100 m).

Herbs 0.2–0.8 m tall, leafy stems terete, 2–6 mm thick, subglabrous to villous with reddish brown hairs 0.5-2 mm long; stipules 1-3 mm long, thin, deciduous. Leaves opposite, subglabrous to villous, lamina obovate to elliptic-obovate or narrowly obovate, $7-23 \times 3-9$ cm, base cuneate and decurrent to form a wing along the petiole, attenuate or abruptly rounded and subauriculate at the base, apex acute to acuminate, 2° veins 6-12 pairs; petioles 2-12 mm long. Inflorescences axillary, 2-6 per node, 2-5 cm long, flowers in a close cymose grouping or paniculate, peduncle 10-27 mm long, villous to subglabrous. Flowers on pedicels 1-4 mm long, hypanthium 2-4 mm long, villous with hairs 1-2 mm long, calyx lobes 2-4 mm long, narrowly triangular; corolla funnelform, 8-16 mm long, white with pink tips to pinkish red, with few distal tri16 Novon



Figure 1. Hoffmannia dwyeri W. Burger. —A. Flowering stem. —B. Flower. A based on Hammel 7412 (F) and Sytsma et al. 4836 (MO); B from Hammel 7412 (MO).

chomes, tube 4–5 mm long; anthers ca. 3.2 mm long, subsessile; style ca. 9 mm long, stigma ca. 3 mm long, broadly ovate. Fruits oblong, 8–9 mm long, 5–6 mm thick, pink to red-magenta, spongy, seeds blue.

Hoffmannia dwyeri has an unusual characteristic: the leaf base is cuneate-decurrent and the winged margins are often revolute near the base, forming a partly enclosed space abaxially. Its short herbaceous habit, long reddish brown multicellular hairs (when present), short densely flowered inflorescences, prominent calyx lobes, relatively large

corolla, and broad stigmatic lobes are additional distinguishing features. Pubescence and floral morphology are similar to *H. valerii* Standley, but that species differs in the form of the lamina base and petiole, and its lower elevation habitat. The new species has only been collected around the Cerro de Pate Macho and upper headwaters of Río Palo Alto, between 1700 and 2100 m elevation. It flowers in March–June.

John Dwyer, who studied *Hoffmannia* intensively over more than 20 years, recognized material of this species as new in two of his annotations but did not publish either of the names. Because Dwyer's

(1969, 1980) publications and many identifications have been so helpful to all those working with this very difficult genus, it seems especially fitting that a distinctive species should bear his name.

Paratypes. PANAMA. Chiriquí: vicinity of Boquete; Cerro Pate de Macho, SW slope, 1800–1950 m, 19 June 1987, Croat 66403 (MO); Río Palo Alto road to Chiriquí border with Bocas del Toro Province near peak of Cerro Pate Macho, 6200 ft., 20 Nov. 1978, Hammel 5814 (MO); end of road past Palo Alto to Bocas, 6200 ft., 18 Mar. 1979, Hammel 6510 (MO); Palo Alto, 4.5 mi. NE of Boquete, forest along western branch of headwaters of Río Palo Alto, 6300 ft., 24 May 1979, Hammel 7412 (MO); S slopes of Cerro Pate Macho along Río Palo Alto, 1300–1800 m, 11 Nov. 1981, Knapp et al. 2083 (MO); trail to Cerro Pate Macho, above Palo Alto, 1700–2100 m, 15 Mar. 1982, Knapp et al. 4249 (MO); SE slopes and summit of Cerro Pate Macho, 4 km NE of Boquete, 1700–2100 m, 26 May 1981, Systma et al. 4836 (MO).

Hoffmannia fortunensis Dwyer ex W. Burger, sp. nov. TYPE: Panama. Chiriquí: S.O. del campamento de Fortuna (Hornito), sitio de presa subiendo hasta la finca Pittí, 1000–1200 m, 14 ago. 1976, M. D. Correa, R. Dressler & C. Garibaldi 2415 (holotype, PMA not seen; isotypes, F, MO).

Suffrutices ad 2 m alti, caulibus teretibus, glabris. Folia ad 23 cm longa, lamina anguste lanceolata, glabra, in sicco discolor, venis lateralibus 9–15 paribus. Inflorescentiae brevi. Flores glabri, lobis calycis brevibus, corollis 4–7 mm longis. Fructus maturi non visi.

Slender shrubs 0.5–2 m tall, leafy stems 2–7 mm thick, terete, glabrous. Leaves opposite, blades 11–23 cm long, 1.5–8 cm wide, linear-lanceolate to narrowly ovate-elliptic or elliptic-oblong, chartaceous, dark above, grayish beneath, glabrous, base cuneate and decurrent, apex acute to acuminate, 2° veins 9–15 pairs, loop-connected along the margin, petioles 15–65 mm long. Inflorescences 1–3 per axil, at lower or leafless nodes, racemose, 3–9 cm long, glabrous, drying dark, peduncles 2–4 cm, 0.3–0.4 mm thick. Flowers glabrous, pedicels to 10 mm long, hypanthium 2–3 mm long, calyx lobes 0.2–0.5 mm long, corolla 4–7 mm long, pale green

or reddish green, corolla tube 1.5–2 mm long; anthers 2.5 mm long. Mature fruits not seen.

The usually long petioles and very narrow leaves with clearly demarked loop-connected secondary veins close to the lamina margins are distinctive features. In addition, the leaves often dry very dark above and grayish beneath. Slender racemose inflorescences with a single rachis drying dark, small flowers, and restriction to the Fortuna area of the Chiriquí highlands between 1000 and 1500 m elevation are additional distinctions. This species appears to be related to *Hoffmannia laxa* Standley, with which it shares the slender glabrous inflorescences and small flowers. There may be lower-elevation collections that have a few characteristics of both species, such as *von Wedel 2363* (MO).

Paratypes. PANAMA. Chiriquí: vicinity of Gualca 11 mi. from Planes de Hornito, La Fortuna on road to dam site, elev. 4000 ft., 9 July 1980, Antonio 5050 (MO); N.O. del Campamento Fortuna (Hornito), 1000–1200 m, 16 ago. 1976, Correa et al. 2515 (MO); Fortuna dam site, forest area, 1400–1600 m, 15 Sep. 1977, Folsom et al. 5568 (MO); near site of dam, lower slopes of Cerro Fortuna, 1150 m, 18 June 1982, Knapp & Vodicka 5584 (MO).

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